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DO GENERALIST TIGER SWALLOWTAIL BUTTERFLY FEMALES SELECT DARK GREEN LEAVES OVER YELLOWISH – OR REDDISH-GREEN LEAVES FOR OVIPOSITION?

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ABSTRACT

In late August and September, using leaves from the same branches, the polyphagous North American swallowtail butterfly species *Papilio glaucus* L. (Lepidoptera: Papilionidae) is shown to select mature dark green leaves of their host plants white ash, *Fraxinus americana L.* (Oleaceae) and tulip tree, *Liriodendron tulipifera* L. (Magnoliaceae) rather than the pale green or yellowish-green mature leaves in laboratory oviposition arenas. In early August, similar results were observed for black cherry, *Prunus serotina* Ehrh. (Rosaceae). Dark green leaves were preferred over light green and yellowish green leaves. These green leaves of black cherry were the most nutritious leaves for larval growth indicating a clear correlation between adult preference and larval performance on this plant. However, tulip tree leaves in the summer did not elicit different oviposition responses between green and light green leaves. A field evaluation of oviposition preferences for young expanding reddish leaves of red bay, *Persea borbonia* (L.) Spreng (Lauraceae) versus slightly older expanded green leaves of the same branch also suggested avoidance of "young" red leaves in Florida by *Papilio troilus* L. and *Papilio palamedes* Drury during the spring season (March-April).

Many intrinsic factors (e.g., female age, time since last oviposition, egg load, time since last mating; Singer 1983, Miller and Strickler 1984, Bossart and Scriber 1999) and extrinsic factors (plant volatiles, leaf color, texture, leaf shape, contact chemosensory cues, and species of host plant) influence the choice of host plant by ovipositing females (Courtney and Kibota 1990; Thompson and Pellmyr 1991; Carter et al. 1999; Frankfater and Scriber 1999, 2003; Renwick 2002; Mercader and Scriber 2007). Additional ovipositional-determining factors not directly related to the plant may include avoidance of natural enemies (Redman and Scriber 2000, Murphy 2004), microclimate temperature and/or humidity preferences (Grossmueller and Lederhouse 1985), and seasonal thermal constraints on voltinism which can select for the most nutritious hosts (Nylin 1988, Scriber and Lederhouse 1992). Lack of availability or low abundance of some host species can also result in local host plant preferences (Rausher 1978, Fitt 1986, Scriber 1986, Scriber et al. 2006).

The selection of host plants by polyphagous species is governed both by factors affecting the rank order of preference and also by the "specificity" (Courtney and Kibota 1990, Mercader and Scriber 2005, 2007). It has been seen that *Papilio glaucus* L. generally selects (specializes on) the host plant species that support fast larval growth in thermally-constrained areas (thus allowing the possibility of an extra generation), but use a wider array of potential hosts in thermally-relaxed areas (i.e., where enough Degree-days accumulate seasonally to complete development of the extra generation on all host plant species, even those of rather low suitability/nutritional quality; Scriber and Lederhouse 1992). This voltinism-suitability hypothesis suggests that preference performance

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relationships may exert strong selection pressures, where allelochemical toxin barriers are not involved, interacting with leaf nutritional quality (bottom up regulation) and natural enemies (top-down regulation).

We know that different species of tree leaves differ in their ability to support growth of lepidopteran species (Scriber and Slansky, Jr. 1981, Slansky, Jr. and Scriber 1985, Mattson and Scriber 1987). The seasonal variation in leaf suitability (Scriber 1984) has less frequently been evaluated for its impact on host selection (Finke and Scriber 1988). The neural limitations hypothesis of host selection (Bernays 2001) predicts that polyphagous species incur costs in the form of prolonged decision making time and increased error rates in host selection relative to more specialized insects. Therefore, the ability of polyphagous insects to detect differences in host plant quality is expected to be lower, as has been previously noted in other butterfly species (Janz and Nylin 1997). Given the likely constraints on information processing in the highly polyphagous *P. glaucus*, we used 2-choice oviposition arenas to determine if *P. glaucus* was capable of selecting between leaves that were light green or reddish-green versus leaves (fully expanded, but) with dark green color, as would be encountered late in the growing season. It is known that for black cherry trees different colors reflect different leaf water and nitrogen content which declines seasonally in green leaves (from 5.1% Nitrogen and 80% water) to 1.5 - 2.0% N and 65% water in yellowish green leaves, and less nitrogen (<1%) and water (<55%) in reddish green, yellow-brown leaves (Scriber 1977). The correlations of color (possibly with nutritional value) and oviposition preference of *Papilio* females for green leaves over yellowish-green mature leaves in the fall and potential toxins/deterrents for younger expanding reddish spring leaves are addressed here.

MATERIALS AND METHODS

Most *P. glaucus* oviposition assays were conducted using wild females of *P. glaucus* collected in Clinton Co. and Allegan Co. in southern Michigan. Due to small sample sizes black cherry assays were supplemented using females obtained from Clarke Co. Georgia and sent to our lab by Express Mail.

Oviposition preferences using leaves from the same branches were conducted in the Fall (September, when most leaves were changing color) using white ash (*Fraxinus americana* L.; n = 5 females) and tulip tree (*Liriodendron tulipifera* L.; n = 9 females). In mid-August, again using leaves from the same braches light green and dark green black cherry leaves (*Prunus serotina* Ehrh.; n = 10 females) and green versus light green tulip tree leaves (n = 8 females) were assessed. Leaf petioles were inserted into water-filled vials with rubber caps, and the leaves were draped along the inside wall of clear, round, large plastic dishes on rotating platforms in front of a bank of incandescent lights (Fig. 1; Scriber 1993). Adults were fed using a 15% honey water solution and eggs were counted and removed daily. Only females laying 9 or more eggs were included in the analyses. The proportion of eggs laid on each leaf was compared within each paired comparison using Bonferroni corrected Paired Wilcoxon Tests using the R Statistical Package V 2.4 (R Development Core Team 2006) with a 0.05 alpha level to test if there were differences in preference between leaves of different ages.

A similar ovipositional study was conducted in late summer, using light green and dark green leaves of black cherry and tulip tree. The eggs from two laboratory reared families that originated from individuals collected in Clarke Co. Georgia were held at 27°C and newly hatched neonate larvae were transferred using camel hair brushes to host plant leaves. Larvae from the two families were reared at 24°C (18:6 h L:D photoperiod) on green (n = 14 from one family and n = 26 from the other family) and light green or yellowish-green (n = 14 and n = 18, respectively) cherry leaves, similar to those used in oviposition assays and weighed ten days after emergence. We tested the effect of leaf age

(green or yellowish-green black cherry leaves) on larval growth with a Nested ANOVA (leaf age nested within larval family) using the R statistical package V 2.4 (R Development Core Team, 2006).

In addition to these lab experiments, we evaluated the differences in field oviposition preferences between "new" expanding reddish leaves compared to more fully-expanded slightly older green leaves of red bay for *Papilio palamedes* Drury and *Papilio troilus* L. during the spring (late March - early April) in Levy Co. and Highlands Co. Florida.

RESULTS

In studies done in September, when the leaves of most trees were beginning to change color, females of *P. glaucus* presented with a choice of light green (or yellowish-green leaves) and dark green leaves from the same branch of white ash trees, showed a clear preference for the green leaves (Figure 1). Nine females that laid 9 or more eggs all placed the majority (84.6%) of these on the green versus yellowish-green leaves (Fig 2A). The same result was obtained for 5 females offered tulip tree leaves (Figure 2B); few were placed on the light green or yellowish-green leaves and most (95.5%) were placed on the green (from the same branches).

In the second study (conducted in August), using black cherry and tulip tree. Females placed in assays with green and yellowish-green black cherry leaves (n = 10) selected green leaves about three times as often as yellowish-green leaves (72.8 ± 5.5 vs. 27.2 ± 5.5, mean ± SE, Figure 2C). However, these summer assays with tulip tree leaves showed mixed results with no strong preference for dark green versus light green tulip leaves (Figure 2D and 3B).

The growth rates of resulting neonate larvae on these green and light green leaves verified that suitability for larval growth was better on the dark green leaves than on the yellowish-green leaves of black cherry (Fig. 3A). The means ± SE for family #20196 and 20192 for larval weight were significantly higher on the green (97.5 ± 6.8 mg) versus the yellowish-green leaves (64.6 ± 5.1 mg) at 10 days ($F = 199.59$, df = 1, 1, $P = 0.04$).

In Highlands County, Florida the newly expanding red bay (*Persea borbonia* (L.) Spreng.) leaves were red or reddish-green, and a careful search of more than 1500 such red bay leaves from 21 different trees in March 2007, yielded no eggs or larvae of *Papilio*. However, very often on the adjacent one or two more expanded green leaves larvae were found feeding and resting in leaf rolls. Sixteen neonate and early instar larvae and one egg were found on green leaves (of more than 2500 searched) of these same 21 trees. Apparently the ovipositing *P. troilus* and *P. palamedes* avoid these red leaves of red bay (Fig. 4). Over a three year period in Levy Co. Florida, eggs of *P. glaucus* were found on young (still expanding) green ash (*Fraxinus pennsylvanica* Marshall) leaves (> 15 eggs or neonates on more than 2000 leaves), but not on any young reddish-green leaves of the same branch (Fig 5).

DISCUSSION

We have shown here that female oviposition preferences of *P. glaucus* are for greener leaves rather than light green, yellowish-green, leaves of black cherry and white ash (Figs 1 & 2). *P. glaucus* females also prefer green over yellowish-green tulip tree leaves in the fall, but in the summer they do not always prefer green over light green leaves from the same branch (Fig 2). This might indicate that cues between these August tulip tree leaves are insufficiently different to be distinguished or of similar chemistry. It seems that this generalist butterfly discerns host quality through contact chemoreception since volatiles would be confused/confounded in these multi-choice lab arenas.

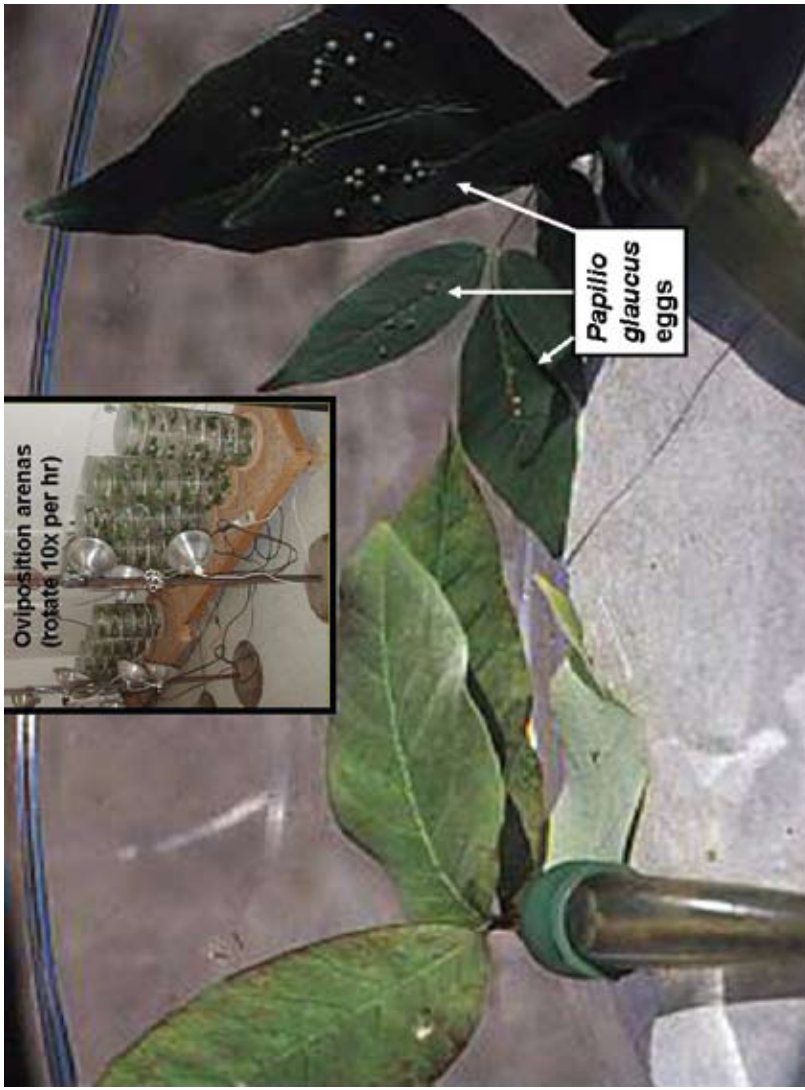

Fig. 1. The experimental oviposition arena showing eggs on the dark green but not on the yellowish-green ash leaves. The inset shows the stacks of arenas on the turntable in front of the light bank.

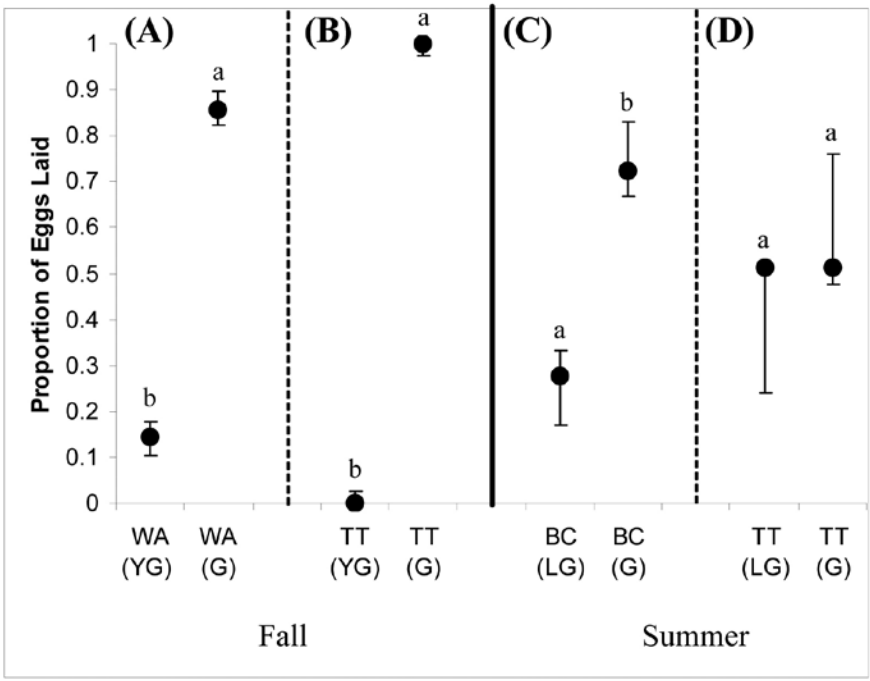

Fig. 2. A). Median proportion of eggs laid by *P. glaucus* butterflies using green (G) and yellowish-green (YG) leaves of white ash (WA) in the fall. B). Median proportion of eggs laid by *P. glaucus* butterflies using green (G) and yellowish-green (YG) leaves of tulip tree (TT) in the fall. C). Median proportion of eggs laid by *P. glaucus* butterflies using green (G) and light green (LG) leaves of tulip tree. D). Median proportion of eggs by *P. glaucus* butterflies using green (G) and light green (LG) leaves of black cherry (BC). In each panel, bars around the medians represent the inter-quartile ranges. Pairwise differences between proportions of eggs laid on each leaf were analyzed separately for each leaf species using Paired Wilcoxon tests. Leaves within each panel with the same letter did not have a significant difference at a Bonferroni corrected $\alpha < 0.05$.

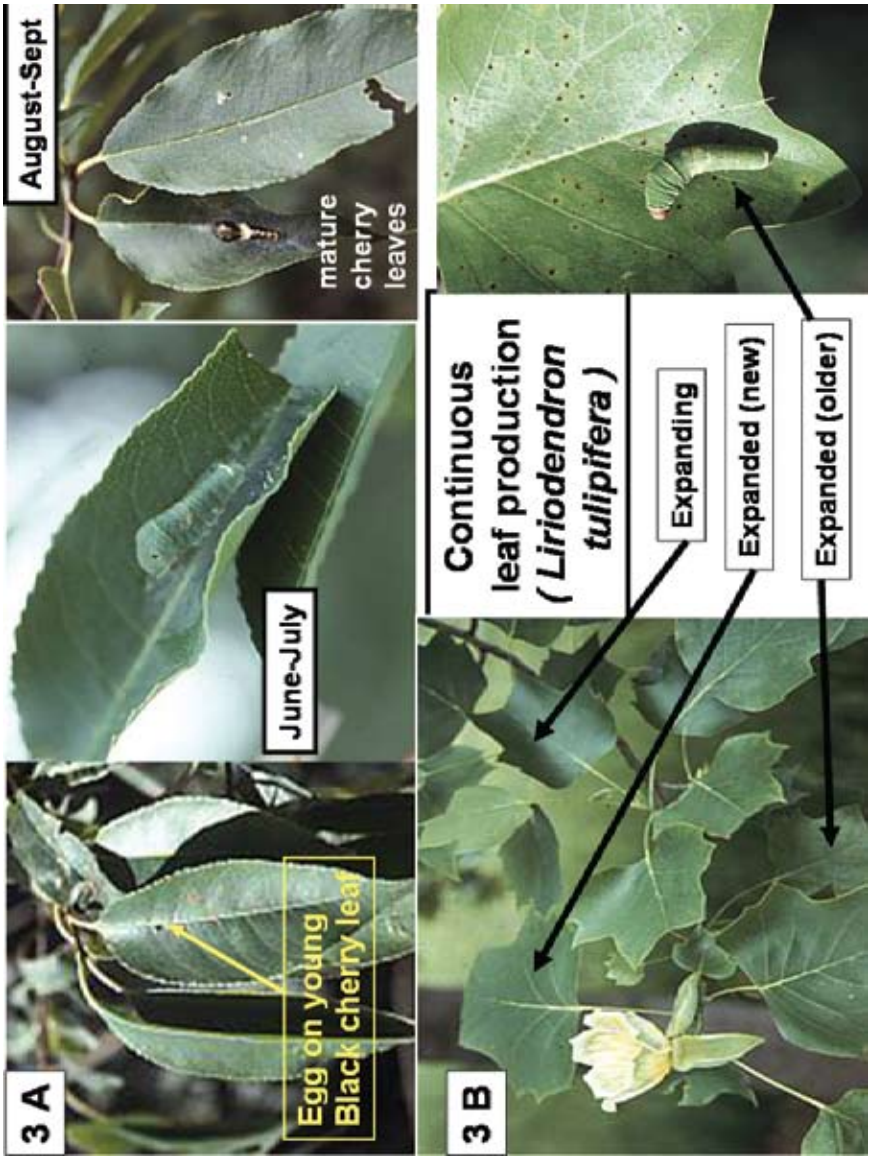

Fig. 3. A). Black cherry showing fully expanded (new) and fully expanded (over-mature) leaves. B). Tulip tree leaves showing the indeterminant growth, with continuous production of new leaves.

Fig. 4. Red bay leaves which had *Papilio* eggs deposited and larvae feeding on the green, but not on the red leaves (March 24-27, 2007; Highlands Co. Florida). Both *P. palamedes* and *P. troilus* form leaf rolls during all instars on red bay (see inset).

Fig. 5. White ash leaves with red expanding tip leaves (Levy Co. Florida; March 2007). Upper right insert shows the new expanded green leaves where eggs are placed and where larvae feed.

White ash and black cherry tree leaves have been documented to show general seasonal decline in the amounts of leaf water and nitrogen seasonally, although tulip tree continuously generates new leaves all season (Scriber and Slansky, Jr. 1981, Scriber 1984). Accelerated differences in the fall can occur with abscission layer formation. In fact, the same branch (of black cherry, for example) can have all stages of leaf quality from dark green (3.2% - 2.8% N and 76% - 65% water), to light green (2.8 - 2.2% N), yellowish-green (2.1 - 1.8% N) reddish-green (1.5% N) and yellow-brown (1.2 – 0.8% N, and <55% water (Scriber 1977, and unpublished). While we did not evaluate the nutritional differences between differently colored tulip tree and ash leaves here, we did determine that the dark green black cherry leaves support a 3-fold faster growth rate than the yellow-green leaves.

Since neonate larvae of these tree-feeding lepidoptera need to start feeding near the location on a particular tree chosen by the mother, it has been assumed that strong selection for highly nutritional oviposition substrates might occur (Zalucki et al. 2002). Even in polyphagous *Papilio* species, the selection of the "wrong" young leaves (i.e., on a toxic, or nearly toxic unsuitable host) could be a fatal "mistake" (Straatman 1962, Wiklund 1975, Berenbaum 1981, Larsson and Ekbom 1995, Renwick 2002, Scriber 2002a, Graves and Shapiro 2003). Consequently, the general lack of correlation of adult oviposition preference and larval growth performance in many, if not most, herbivorous insects has been somewhat of an enigma (Thompson 1988, 1998; Mayhew 2001; Bossart 2003). The reasons for a general lack of genetic linkage of preference and performance remains largely unknown (Bossart and Scriber 1999, Berenbaum and Feeny 2008). However, it is known that abiotic factors can interact with nutritional quality to result in strong preference-performance correlations in *Papilio* in accord with the "voltinism-suitability hypothesis" (Nylin 1988; Scriber and Lederhouse 1992; Scriber 1996, 2002b, 2005). In this scenario, thermal constraints on seasonal degree-day accumulations may (on a poor host) result in fewer generations than might be possible on a host species that supports rapid growth. The selection of the "best" leaves available on a non-toxic host species (Feeny 1995, Scriber et al. 2007) is generally assumed to be always favored, in order to minimize time exposed to natural enemies (predators, parasites, and disease; Slansky, Jr. 1993, Bernays 1998, Scriber 2004) or freeze susceptibility (Fordyce and Shapiro 2003, Tesar and Scriber 2003). However, fast growth is not always possible (e.g., tree leaves are generally poorer than herbaceous plants and roots are notoriously poor in nutritional quality, resulting in slow growth of root feeders, etc. (Slansky, Jr. and Scriber 1985).

From both the ecological and evolutionary perspectives, it remains unclear if rapid growth rates are always selected for (Slansky, Jr. 1993, Benrey and Denno 1997). In addition, adaptations for "compensatory feeding" may be invoked when diets are unbalanced in carbohydrates, protein, energy, or minerals (Scriber 1984, Slansky, Jr. and Scriber 1985, Mattson and Scriber 1987, Simpson and Simpson 1990, Fageria and Scriber 2001, Slansky, Jr. and Wheeler 1992, Trier and Mattson 2003 "diet-induced thermogenesis"). This feeding compensation may be via diet "self-selection" (Waldbauer and Friedman 1991) or "organismal stoichiometry" (Raubenheimer and Simpson 2004). However, larvae can not always compensate for eggs placed on older, over-mature leaves since higher risks as well as slower growth may be involved for the neonate larva, harder to consume and digest leaves, with higher vulnerability to enemies (Ayres and Scriber 1994, Zalucki et al. 2002). These slower growth rates were observed here with *P. glaucus* on older light green or yellowish-green versus newer dark green leaves of black cherry.

Field assessments of green versus younger expanding reddish leaves of red bay in Florida suggest that the Lauraceae-specialized *P. palamedes* and *P. troilus* butterflies avoid "reddish" leaves (Fig. 4). Our extensive searches of 21 trees resulted in no eggs or neonates feeding on red leaves (more than 1500),

but we found 16 neonate larvae and one egg on green leaves (>2500 searched). Similarly, in Florida, *P. glaucus* on green ash prefers green leaves and appears to avoid reddish-green leaves in the spring (JMS personal observation, and Fig. 5).

It is likely that these *Papilio* spp. may be using cues other than gustation to detect host plant quality. It is known, that unlike most invertebrates (Lee et al. 1987), *Papilio* species including *P. glaucus* (Briscoe 2000) have long wavelength red receptors that enable them to see and select green leaves (Kelber 1999). While most invertebrates lack red receptors (Menzel and Backhaus 1991), and peak reflectance from leaf anthocyanins lies in this region of about 630 nm (Lee et al. 1987), notable exceptions with a long wavelength receptor tuned to 610 nm include the Papilionidae (Arikawa and Uchiyama 1996). One species, *Papilio aegeus* Donovan, uses this red receptor to avoid red leaves (Kelber 1999) and, perhaps *P. glaucus* can do the same (Briscoe 2000).

It has been suggested that some young leaves gain a protection from insect herbivores by a "delayed-greening" strategy for newly flushed leaves (which are reddish; Dominy et al. 2002). This "delayed greening" appeared to be true for ash leaves in Levy Co. Florida in 2007 (Fig. 5). This "delayed greening" has been suggested by Coley and Aide (1989) to be due to a high anthocyanin content, which, aside from being red, has fungicidal properties. However, this "delayed greening" may also protect leaves by keeping them devoid of nutritive value until they reach full size (Figs. 4 and 5, Dominy et al. 2002).

Regardless of the ecological/evolutionary advantages of selecting younger nutritious host leaves by *P. glaucus*, the physiological/ chemical mechanisms permitting them to distinguish the best leaves remains unknown. Leaf color may play some unknown role in these *Papilio* as in the related *Battus philenor* L. (Papilionidae), which can learn leaf color and shape (Rausher 1978, Weiss and Papaj 2003, Miller and Strickler 1984). It is known that other *Papilio* species have red receptors to see green (Kelber 1999), as is the case for *P. glaucus* (Briscoe 2000), however, we do not really know if these specific color stimuli were used by the *P. palamedes* and *P. troilus* (or even *P. glaucus*) in these studies. Our ovipositional assays primarily detect differences in contact chemoreception and therefore the responses observed in our assays suggest that females of the polyphagous *P. glaucus* can detect and utilize leaf surface cues correlated with color. In these and related *Papilio*, the final and most important signal seems to come from chemosensory cues to the female tarsi as they taste the leaves before ovipositing (Feeny 1995; Nishida 1995; Frankfater and Scriber 1999, 2003).

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